Biological Services Program
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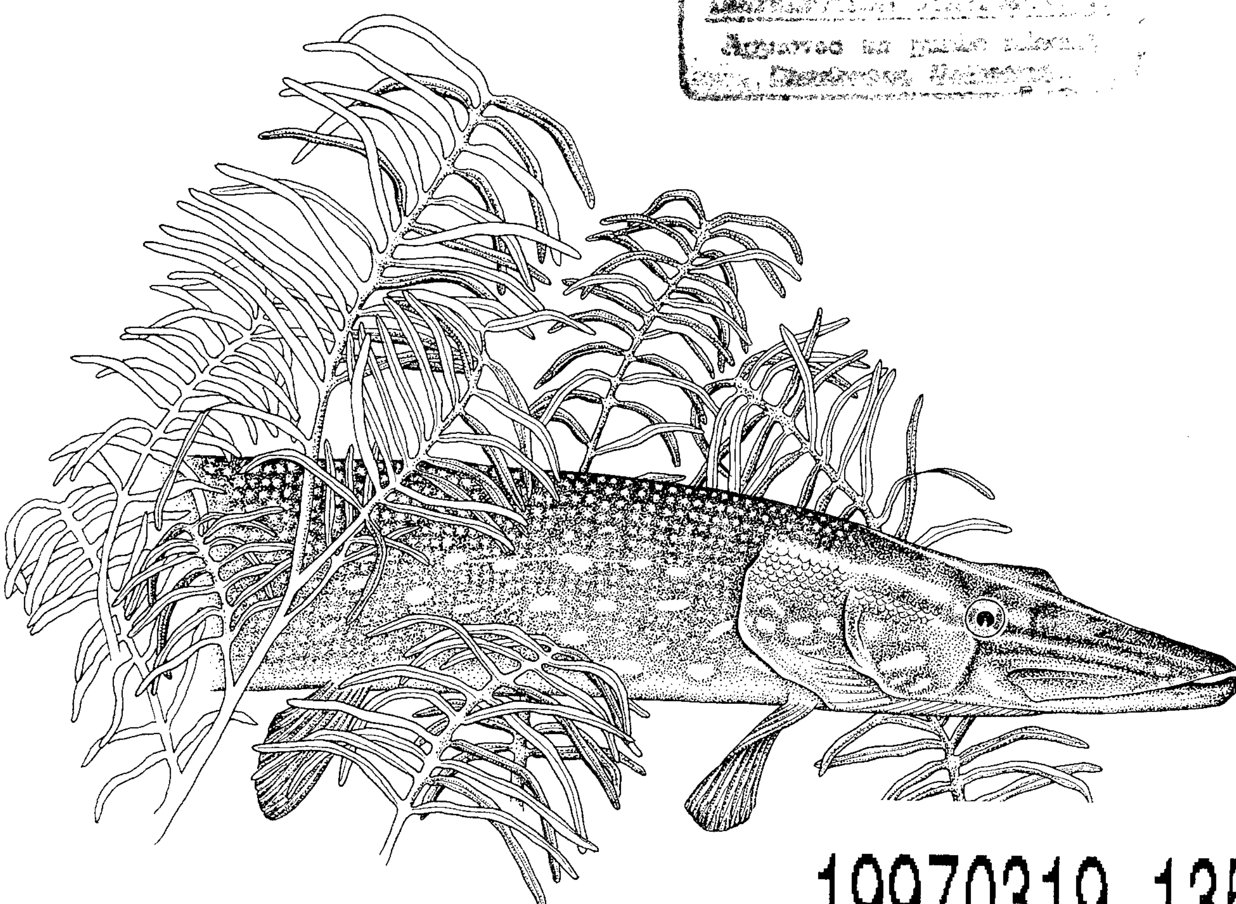
HABITAT SUITABILITY INDEX MODELS: NORTHERN PIKE



Fish and Wildlife Service

U.S. Department of the Interior

The Biological Services Program was established within the U.S. Fish and Wildlife Service to supply scientific information and methodologies on key environmental issues that impact fish and wildlife resources and their supporting ecosystems. The mission of the program is as follows:

- To strengthen the Fish and Wildlife Service in its role as a primary source of information on national fish and wildlife resources, particularly in respect to environmental impact assessment.
- To gather, analyze, and present information that will aid decisionmakers in the identification and resolution of problems associated with major changes in land and water use.
- To provide better ecological information and evaluation for Department of the Interior development programs, such as those relating to energy development.

Information developed by the Biological Services Program is intended for use in the planning and decisionmaking process to prevent or minimize the impact of development on fish and wildlife. Research activities and technical assistance services are based on an analysis of the issues, a determination of the decisionmakers involved and their information needs, and an evaluation of the state of the art to identify information gaps and to determine priorities. This is a strategy that will ensure that the products produced and disseminated are timely and useful.

Projects have been initiated in the following areas: coal extraction and conversion; power plants; geothermal, mineral and oil shale development; water resource analysis, including stream alterations and western water allocation; coastal ecosystems and Outer Continental Shelf development; and systems inventory, including National Wetland Inventory, habitat classification and analysis, and information transfer.

The Biological Services Program consists of the Office of Biological Services in Washington, D.C., which is responsible for overall planning and management; National Teams, which provide the Program's central scientific and technical expertise and arrange for contracting biological services studies with states, universities, consulting firms, and others; Regional Staffs, who provide a link to problems at the operating level; and staffs at certain Fish and Wildlife Service research facilities, who conduct in-house research studies.

This model is designed to be used by the Division of Ecological Services in conjunction with the Habitat Evaluation Procedures.

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HABITAT SUITABILITY INDEX MODELS: NORTHERN PIKE

by

Peter D. Inskip
Habitat Evaluation Procedures Group
Western Energy and Land Use Team
U.S. Fish and Wildlife Service
Drake Creekside Building One
2625 Redwing Road
Ft. Collins, CO 80526

Western Energy and Land Use Team
Office of Biological Services
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

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PREFACE

The habitat use information and Habitat Suitability Index (HSI) models presented in this document are intended for use in impact assessment and habitat management activities. Literature concerning the habitat requirements and preferences of northern pike is reviewed and then synthesized into HSI models, which are scaled to produce an index between 0 (unsuitable habitat) and 1 (optimal habitat). Assumptions used to transform habitat use information into these quantitative models are noted, and guidelines for model application are described. Other models found in the literature which may also be used to calculate an HSI are cited.

Use of these models for impact assessment requires the setting of clear study objectives and may require modification of the models to meet those objectives. Methods for modifying HSI models and recommended measurement techniques for model variables are presented in Terrell et al. (in press).[1] A discussion of HSI model building techniques is presented in U.S. Fish and Wildlife Service (1981).[2]

The HSI models presented herein are hypotheses of species-habitat relationships, not statements of proven cause and effect relationships. The models have not been tested against field population data. For this reason, the U.S. Fish and Wildlife Service encourages model users to send comments and suggestions that may help us increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning. Please send comments to:

Habitat Evaluation Procedures
Western Energy and Land Use Team
U.S. Fish and Wildlife Service
2625 Redwing Road
Ft. Collins, CO 80526

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[1]Terrell, J. W., T. E. McMahon, P. D. Inskip, R. F. Raleigh, and K. W. Williamson (in press). Habitat suitability index models: Appendix A. Guidelines for riverine and lacustrine applications of fish HSI models with the Habitat Evaluation Procedures. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82-10.A.

[2]U.S. Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models. 103 ESM. U.S. Dept. Int., Fish Wildl. Serv., Div. Ecol. Serv. n.p.

CONTENTS

	Page
PREFACE	iii
ACKNOWLEDGMENTS	v
HABITAT USE INFORMATION	1
General	1
Age, Growth, and Food	1
Reproduction	3
Specific Habitat Requirements	4
HABITAT SUITABILITY INDEX (HSI) MODELS	12
Model Description - Lacustrine and Riverine	12
Model Applicability	15
Suitability Index (SI) Graphs for Model Variables	17
Development of Suitability Index Graphs: Rationale and Assumptions	21
Field Use of the Model	25
Interpreting Model Outputs	28
ADDITIONAL HABITAT MODELS	28
REFERENCES	29

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NORTHERN PIKE (*Esox lucius* Linnaeus)

HABITAT USE INFORMATION

General

Northern pike (*Esox lucius*) occur worldwide in fresh waters north of 40° N (Toner and Lawler 1969). It is the only species in the esocid family native to both North America and Eurasia (Scott and Crossman 1973). The native North American range included Alaska, most of Canada south of the Arctic Circle (excepting most of British Columbia), the Missouri River drainage, the Mississippi River drainage upstream of the confluence with the Missouri, the Ohio River drainage in Pennsylvania and New York, and the Great Lakes drainage basin; the southern limit was probably in central Missouri (Crossman 1978). Northern pike distribution has expanded with their introduction into impoundments outside of their native range, most commonly in Great Plains and Rocky Mountain States (McCarraher 1961; Carlander et al. 1978). Lakes account for most of the North American habitat of northern pike (Carlander et al. 1978; Crossman 1978).

Age, Growth, and Food

Growth rate of northern pike is highly variable, both among and within populations. There is a general inverse relationship between growth rate and north latitude over a latitudinal gradient spanning the United States and Canada (Miller and Kennedy 1948; Crabtree 1969; Vasey 1974), but the trend is not always strongly defined over limited geographic areas (Diana, pers. comm.). Temporal variability in growth rate, associated with changes in density of northern pike and likely prey species, has also been noted (Kempinger and Carline 1978). Individual growth rates can vary considerably within a single cohort. Young of the year northern pike, stocked as fry in a Michigan rearing pond in early May and recovered the following October, ranged in length from 8.3 to 44.6 cm (Carbine 1945).

The age at which northern pike become sexually mature depends on their growth rate. Male northern pike are typically 34 to 42 cm (total length) and females 40 to 48 cm when they spawn for the first time (Frost and Kipling 1967; Priegel and Krohn 1975). In Great Bear Lake (Northwest Territories), this translates to age 5 or 6 for males and age 6 or 7 for females (Miller and Kennedy 1948). In Wisconsin, age 2 (males and females) is more typical (Priegel and Krohn 1975). One-year old spawners are not unusual in Kansas (Schryer et al. 1971), Missouri (Vasey 1974), and Texas (Crabtree 1969) reservoirs, where growth is rapid.

Longevity and age-specific fecundity are also related to growth rate. Ten-year old and older northern pike are not uncommon in northern Canadian and Alaskan lakes, where growth is slow, and individuals as old as 24 years have been recorded (Miller and Kennedy 1948; Rawson 1959; Alt 1969). Populations in Wisconsin (Van Engel 1940) and more southern waters (Buss and Miller 1961; Schryer et al. 1971) are composed mostly of 4-year old and younger fish. Fecundity increases exponentially with length and proportionally with weight (Carbine 1944; Frost and Kipling 1967; Priegel and Krohn 1975). Carbine (1944) reported an average fecundity of 32,200 eggs for 30 pike between 40 and 89 cm (total length).

Northern pike become piscivorous very early in life. Fry begin to feed approximately 10 days after hatching, on reaching a length of 10 to 12 mm (Hunt and Carbine 1951; Franklin and Smith 1963). The diet initially consists of zooplankton but quickly broadens to include aquatic insect larvae and then fish (Hunt and Carbine 1951; Frost 1954; McCarraher 1957; Fago 1977). By the time the fry reach 50 to 60 mm, typically within 4 to 5 weeks after hatching in the northern Midwest (Franklin and Smith 1963; Fago 1977) and Northeast (Forney 1968), fish comprise most of the diet (Hunt and Carbine 1951; Frost 1954). Fry are cannibalistic at sizes as small as 21 mm (Hunt and Carbine 1951).

Fish continue to predominate in the diet throughout the remainder of the life history, but northern pike occasionally prey on leeches, aquatic insects, crayfish, waterfowl, and small mammals (Frost 1954; Lagler 1956; Seaburg and Moyle 1964; Lawler 1965; Mann 1976). Northern pike feed opportunistically, exploiting seasonally abundant food sources (Frost 1954; Lawler 1965; Wagner 1972). Soft-rayed, cylindrical fishes are apparently more easily swallowed than are spiny and/or laterally compressed species (Frost 1954; Hoogland et al. 1957; Beyerle and Williams 1968; Johnson 1969; Mauck and Coble 1971; Wagner 1972; Weithman and Anderson 1977; Wolfert and Miller 1978). Gizzard shad (*Dorosoma cepedianum*) (Wagner 1972), alewife (*Alosa pseudoharengus*) (Wolfert and Miller 1978), yellow perch (*Perca flavescens*) (Lawler 1965; Johnson 1969; Diana 1979), and trout-perch (*Percopsis omiscomaycus*) (Lawler 1965) have been noted as being especially common in the diet. White suckers (*Catostomus commersoni*) are commonly eaten by large northern pike (Lawler 1965; Koshinsky 1979).

Reports of cannibalism among juvenile and adult northern pike are not unusual, but, in most cases, it accounts for a minor part of the diet (Frost 1954; Lawler 1965; Johnson 1969; Wagner 1972; Mann 1976). Alt (1968) described a notable exception; he found that the diet during summer and early fall consisted primarily of northern pike in several Alaskan lakes. Dryden and Jessop (1974) reported a high incidence of cannibalism among northern pike captured during a spawning run in a stream in the Northwest Territories. It appears that cannibalism occurs more frequently in waters with few fish species than in those where the fish community is diverse.

Northern pike are visual predators (Polyak 1957; Braekevelt 1975) and are primarily day active (Carlander and Cleary 1949; Diana 1980). Their ambush style of hunting requires cover, usually sought in the form of aquatic plants. Tree stumps and fallen logs may also be used (Crossman, pers. comm.).

Consumption rate varies seasonally. Maximum rates usually occur in spring or early summer (Johnson 1966a; Weithman and Anderson 1977; Diana 1979), following the spawning period. Weithman and Anderson (1977) observed peak feeding at temperatures between 15 and 18° C for yearling northern pike held under experimental conditions; there was a summer reduction in consumption rate between May and September highs.

Reproduction

Northern pike spawn in spring, shortly after ice-out, when the water has warmed to 8 to 12° C (Embody 1918; McNamara 1936; Clark 1950; Fabricius and Gustafson 1958; Franklin and Smith 1963; June 1971; Priegel and Krohn 1975). Movement to spawning grounds often begins before all ice has melted. Upstream spawning migrations out of lakes in Michigan (Carbine 1942) and Minnesota (Franklin and Smith 1963) occurred as soon as there was sufficient clearance between inshore ice and the bottom to permit passage. Robertson (1969) observed that upstream movement of northern pike was interrupted when the water temperature dropped below 5.5° C. Isolated spawning may occur at temperatures less than 8° C (McNamara 1936; Clark 1950; Schryer et al. 1971). Most females have completed spawning by the time temperatures exceed 13° C (Schryer et al. 1971).

Spawning occurs over vegetation in areas of calm, shallow water (Williamson 1942; Clark 1950; Fabricius 1950). There is a strong tendency to migrate up tributaries to flooded marshes, wetlands, or shallow pools among both lake (Carbine and Applegate 1948; Schultz 1955; Robertson 1969; Koshinsky 1979) and river (Harrison and Hadley 1978) populations. Flooded terrestrial vegetation (McCarraher and Thomas 1972) and shallow, weedy bays or backwaters may also be used (Jarvenpa 1962a; Frost and Kipling 1967). The absence of inundated vegetation can inhibit or delay spawning (Fabricius 1950; Fabricius and Gustafson 1958). The timing of spawning has been linked to water level changes (Fabricius 1950; June 1970, 1971, 1977).

Spawning groups, consisting of a female plus one, or more typically, several, males move continually. Only a few eggs, 5 to 60 according to Svardson (1949), are released at any one spot (Svardson 1949; Clark 1950; Fabricius and Gustafson 1958). Gametes are broadcast (Fabricius and Gustafson 1958), and no parental care is provided (Eddy and Underhill 1974). Eggs adhere to vegetation (Fabricius and Gustafson 1958; Frost and Kipling 1967). Both laboratory (Fabricius and Gustafson 1958) and field (Koshinsky 1979) observations indicate that spawning occurs in distinct series of mating acts, between which the fish are stationary, presumably to rest. Spawning groups may cover considerable distances before all eggs are released (Koshinsky 1979). Distances between egg releases are likely to be greater when the distribution of spawning habitat is patchy (Fabricius and Gustafson 1958). Northern pike do not spawn at night (Clark 1950; Fabricius and Gustafson 1958). Spawning may be interrupted by cold weather, water level drawdowns (Clark 1950; Fabricius and Gustafson 1958; June 1970), strong wind, or rain (Koshinsky 1979). Prolonged interruptions may result in resorption of eggs (June 1970).

Areas used for spawning can be far away from areas inhabited during the rest of the year. Northern pike tagged on spawning grounds in a Missouri River reservoir were later recaptured up to 322 km away; most, however, were caught within 32 km of the site where they were tagged (Moen and Henegar 1971). Pike tagged during the upstream spawning run out of a Michigan lake were subsequently recaptured up to 15 km away in the lake (Carbine and Applegate 1948).

The degree to which northern pike home to particular spawning grounds is unclear. Tagging and meristic studies of northern pike in Lac La Ronge, Saskatchewan, suggested the presence of separate populations within the lake, but it is not necessary to postulate a homing instinct to account for this observation (Koshinsky 1979). The northern pike did not disperse far from the mouths of tributaries used for spawning. In spring, they may simply have moved up the nearest suitable stream (Koshinsky 1979). Frost and Kipling (1967) also gave evidence of repeated use of a spawning area in a lake in England, but their results did not conclusively demonstrate homing. Miller (1948) reported movements of several northern pike among widely separated (2.4 to 3.2 km) spawning areas within a 10-day period. He did not note whether the fish were ripe at each capture location. Franklin and Smith (1963) concluded that northern pike in a Minnesota lake do not home to particular spawning grounds.

Specific Habitat Requirements

Northern pike are not adapted for life in strong currents. Throughout their range, they occur more frequently in lakes than in rivers (Crossman 1978), where they inhabit backwaters and pools (Christenson and Smith 1965; Kamyshnaya and Tsepkin 1973; Paragamian 1976; Kallemeyn and Novotny 1977). They avoid channelized reaches (Kallemeyn and Novotny 1977). Strong currents (> 1.5 m/s) can block spawning migrations (Dryden and Jessop 1974).

The availability of suitable spawning habitat is the factor which most often excludes northern pike from lakes, reservoirs, and slow moving rivers and which limits abundance where the species does occur. Shallow vegetated areas, such as flooded marshes, flooded terrestrial vegetation, or weedy bays provide suitable habitat, provided that high water levels are maintained throughout the embryo and fry stages (Hassler 1970). Strong year-classes often occur as a newly created reservoir fills and in years when exceptionally high spring water levels flood previously unflooded terrestrial vegetation (Crabtree 1969; Cooper 1971; June 1976; Groen and Schroeder 1978; Nelson 1978). Conversely, weak year-classes in impoundments and natural environments are associated with low water levels (Johnson 1957; Cooper 1971; Schryer et al. 1971; Rundberg 1977; Nelson 1978; Stewart 1978). Northern pike do not do well in reservoirs with widely fluctuating water levels (Wajdowicz 1964) because nearshore vegetation does not develop. Long term reductions in the abundance of northern pike have accompanied the draining and filling of wetlands (Brynildson 1958; Threinen 1969; Baumann et al. 1974; Forney 1977), reductions in the density of aquatic plants (Hurley and Christie 1977; Ciepielewski 1981), and blocking of access to spawning grounds (Trautman 1957). Fishery managers in Michigan were able to substantially increase

populations of adult northern pike in a set of lakes by enhancing the quality and quantity of spawning habitat (Williams and Jacob 1971).

Young northern pike eventually disperse from spawning areas, but pike of all ages continue to frequent shallow areas with vegetation. Small pike are especially dependent on this habitat. Growth and food conversion efficiency of young pike kept in tanks with no vegetation were erratic; pike kept in ponds with no vegetation resided in any areas that provided cover (Johnson 1960). The minimum size of northern pike captured in gill nets in Lac La Ronge was positively associated with depth, but the maximum size was not, indicating that large pike use a wider range of depths than do small pike (Koshinsky 1979). Nine tagged northern pike (1.6 to 4.1 kg) in an eutrophic Alberta lake generally remained in areas with submerged and emergent aquatic vegetation, in water shallower than 4 m, and within 300 m of shore (Diana et al. 1977). Northern pike in a Michigan lake, that were tagged at spawning time and subsequently recaptured by anglers, were caught almost exclusively in weed beds (Carbine and Applegate 1948). Ninety percent of the pike captured in a gill netting survey of Great Slave Lake in northern Canada were caught within 400 m of shore, and very few were taken at depths greater than 10 m (Rawson 1951). Fisheries surveys in lakes of the Churchill River basin in northern Saskatchewan also indicated that pike mostly inhabit water shallower than 10 m, although they occur at least as deep as 27 m (Dean 1975; Liaw and O'Connor 1975; Koshinsky 1979).

Depth <u>per se</u> does not appear to be the factor determining depth distribution of northern pike. Depth distribution appears to be in response to differences in temperature, dissolved oxygen, vegetation, and food. Northern pike rarely venture below the thermocline (Reighard 1915; Pearse 1922; Rawson 1951). In Douglas Lake, Michigan, a well-defined thermocline typically forms at a depth of 12.2 to 13.7 m; 13.7 m was the maximum depth at which northern pike were captured (Reighard 1915). The other northern pike collected in this study were caught at depths $\leq$ 7.9 m, which coincides with the lower (lakeward) depth limit of aquatic vegetation. Eleven of these 21 pike were caught at depths between 7.6 and 7.9 m, perhaps indicating that pike prefer the interface between vegetation and open water (Reighard 1915). Underwater observations of northern pike in an Alberta lake also indicated an attraction to this boundary zone (Chapman and MacKay, in prep.). The edges of vegetated areas would provide good cover for feeding activities.

Northern pike are a coolwater species (Casselman 1978). Their occurrence over a broad latitudinal belt, circa 40 to 70° N in North America (Karvelis 1964), however, demonstrates their adaptability to a variety of thermal regimes. For example, the average maximum summer temperature in the limnetic zone of Great Bear Lake (Northwest Territories) is 5 to 7° C, and the ice free season usually lasts less than 19 weeks (Johnson 1966b). Temperatures may reach 16° C, at least briefly, in protected bays, where most northern pike occur (Miller 1947). Lake Mendota, in southern Wisconsin, typically warms to about 24° C, with an ice free season of 36 to 40 weeks (Juday 1940).

Summer habitat for northern pike is limited in some lakes by a combination of high surface temperatures and low oxygen concentrations in cooler, deeper strata. Krohn (1969) reported a mid-August die-off in a Wisconsin lake following several very warm days. Temperatures ranged from 32° C at the surface to 24° C at a depth of 3.7 m, the lower limit of oxygenated water. High surface temperatures (32° C) coincided with the beginning of a northern pike die-off in a Missouri reservoir (Goddard and Redmond 1978). Dead fish were found to have bacterial, fungal, and protozoan infections. High surface temperatures can contribute to high incidences of infection by lowering resistance to disease and by concentrating the pike in a narrow depth stratum. Substantial mortality of northern pike occurred in an Iowa marsh when temperatures reached 35.6° C at the surface and 31.7° C at the bottom (Ridenhour 1957). In this case, oxygen concentrations were adequate, but temperatures were too high at all depths.

It seems likely that high summer and/or winter temperatures limit the southern distribution of northern pike. Although present in the Mississippi River drainage, pike are absent from waters south of the 32.2° C isotherm for normal July daily maximal air temperature, except in thermally stratified reservoirs where they have been introduced (Visher 1954; Crossman 1978). Northern pike are absent from all but the upper reaches of the Ohio River and its tributaries, although muskellunge (*Esox masquinongy*), a closely related species with similar spawning habitat requirements, are widely distributed in the drainage (Forbes and Richardson 1920; Gerking 1945; Trautman 1957; Crossman 1978). Much of the Ohio River is south of the 31° C isotherm for mean maximal July air temperature (National Oceanographic and Atmospheric Administration 1974). Surface water temperatures of 29 to 31° C are not unusual for Ohio lakes (Tressler et al. 1940). In the laboratory, young northern pike do not grow at temperatures above 28° C, even when fed *ad libitum* (Casselman 1978). Temperatures greater than 32° C can cause death within 2 days (Scott 1964).

High temperatures at other times of the year may limit reproductive success. In a laboratory study, the percentage of yellow perch that spawned was highest when they were exposed to temperatures $\leq$ 6° C for a minimum of 185 days, beginning October 30 (Jones et al., unpublished data cited in Hokanson 1977). No successful spawning occurred among perch held at a minimum temperature of 12° C or higher. Northern pike, which occur farther north than do yellow perch (Scott and Crossman 1973), are presumably also adapted to a seasonal temperature cycle involving cold winters.

Dissolved oxygen concentration is usually the most important habitat variable affecting overwinter survival of northern pike. Shallow, heavily vegetated lakes and rivers with low discharges - habitats that might be quite favorable for northern pike at other times of the year (Johnson and Moyle 1969) - frequently develop low dissolved oxygen concentrations during winter. Laboratory and field observations indicate that pike are more tolerant of low dissolved oxygen conditions during winter than are many other temperate species, including black crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), walleye (*Stizostedion vitreum vitreum*), and yellow perch (Cooper and Washburn 1949; Moyle and Clothier 1959; Patriarche and Merna 1970; Petrosky and Magnuson 1973). If the

change to low dissolved oxygen is gradual, northern pike appear able to tolerate concentrations as low as 0.1 to 0.4 mg/l for at least several days (Cooper and Washburn 1949; Magnuson and Karlen 1970; Petrosky and Magnuson 1973). A prolonged period with dissolved oxygen concentrations less than 1.0 mg/l, however, appears to cause partial or complete winterkill (Johnson and Moyle 1969; Stewart 1978). The critical oxygen concentration also depends on temperature. Requirements for dissolved oxygen increase exponentially as temperature increases, but the lower incipient lethal concentration [concentration below which pike cannot survive for an indefinite time (Fry 1947)] is still relatively low (< 1.5 mg/l) at 28° C (Casselman 1978).

Tolerance of low dissolved oxygen conditions appears to be inversely related to size for juvenile and adult northern pike. Overwinter mortality in an Ontario lake with low oxygen levels was total for pike older than 2 years and/or longer than 39 cm (fork length), but many smaller, younger individuals survived (Casselman and Harvey 1975). Similarly, very few northern pike older than 2 years were present in a Montana stream in which winter dissolved oxygen concentration dropped to low levels, although young fish were common (Stewart 1981).

Fish kills due to low dissolved oxygen concentrations can also occur during summer in shallow, nutrient-rich waters. The cause is often the collapse of a heavy bloom of blue-green algae (Barica 1975). Northern pike were among the many dead fishes observed in a small Wisconsin river when the decomposition of a large algal mass temporarily depleted the dissolved oxygen (Mackenthun et al. 1945).

An extensive review of limnological characteristics of Ontario lakes containing northern pike, walleye, smallmouth bass (<u>Micropterus dolomieui</u>), and lake trout (<u>Salvelinus namaycush</u>), singly and in various combinations, provides a useful overview of northern pike habitat in this region (Johnson et al. 1977). Nearly 70% of the lakes that contain northern pike contain either only northern pike or northern pike and walleye. It appears that lakes with northern pike typically have mean depths of 2 to 6 m, littoral (≤ 6.1 m deep) areas which are 60 to 80% of the total surface area, Secchi disk transparencies of 2 to 4 m, total dissolved solids (TDS) levels between 50 and 125 mg/l, and a near neutral or slightly acidic pH, based on average values of these habitat variables for groups of lakes with different species combinations. These ranges could reflect availability of habitat conditions as well as habitat requirements of northern pike, particularly for water quality parameters. In those lakes where both northern pike and lake trout occur, pike are likely to be largely confined to the perimeter or to island/shoal areas.

Although northern pike occur in oligotrophic waters, they are more typical of mesotrophic or borderline eutrophic conditions (Casselman 1978; Ryder and Kerr 1978). The mean total phosphorus (TP) concentration in Minnesota lakes containing northern pike in association with walleye and yellow perch was 0.034 ppm, compared to 0.02 ppm for lake trout-cisco (<u>Coregonus artedi</u>) lakes, 0.058 for bass-panfish lakes, and 0.126 for "rough fish" lakes; lakes in which northern pike accounted for a significant fraction of the fish population

typically had TP levels ≤ 0.10 ppm (Moyle 1956). Moyle noted that temperature may also explain patterns of fish distribution in Minnesota and cautioned against overemphasis on edaphic factors alone.

Ionic concentrations appear to be directly limiting to northern pike only in coastal and arid environments. Ryder et al. (1974) noted that TDS levels are rarely so low that ions essential for fish metabolism and growth are limiting; these authors speculated that such a limit is near or below 3 ppm, and very few natural waters are that dilute. Waters with high ionic concentrations apparently do limit the distribution of northern pike, but the critical concentration is unknown. Northern pike apparently do not utilize brackish habitats in North America, but there are reports of pike occurring in the Baltic Sea at salinities of 10 ppt and reproducing at salinities of 7 ppt (Svardson, personal communication cited in Toner and Lawler 1969), and pike have been commercially harvested from brackish waters in Finland (Lind 1977). Rawson and Moore (1944) found northern pike in saline Saskatchewan lakes only where TDS levels were less than about 3,500 ppm (roughly equivalent to a salinity of 3.5 ppt). Northern pike are said to have "some tolerance" to TDS levels of 2,200 to 3,800 ppm in alkaline Nebraska lakes (Schoenecker 1970), but pike did not spawn in a Nebraska lake with a TDS level of 1,024 ppm (McCarraher 1962). High concentrations of particular ions may be harmful at salinities which do not cause general osmoregulatory stress. For example, mortality of northern pike embryos and fry is extensive when total alkalinity exceeds 950 mg/l (McCarraher 1971). Until effects of individual ions are clarified, it seems reasonable to assume an upper TDS limit of 3,500 ppm.

Self-sustaining populations of northern pike can persist at pH's as low as 5.0 (Harvey 1980). Lower pH's are damaging to fry. Cumulative mortality of fry held at a pH of 4.2 (range 4.0 to 4.3) was 96.5%, compared to 25.6% mortality at a pH of 5.2 (4.7 to 6.0), and 17% mortality at a pH of 6.8 (6.5 to 7.2) (Johansson and Kihlstrom 1975). Towards the opposite extreme, northern pike occur in lakes with a pH of 8.9 (Rawson and Moore 1944; Priegel and Krohn 1975). Fingerling and larger northern pike can survive pH's in the 9.0 to 9.5 range, but it is not clear whether successful reproduction can occur at the upper limit of this range (McCarraher 1962).

Northern pike grow through a broad size range; tolerances, requirements, and preferences change as they grow. Although most developmental changes are gradual, it is useful to describe habitat requirements for northern pike in terms of four stages: spawning/embryo; fry; juvenile; and adult. These life stages, for purposes of this discussion, are defined as follows:

1. Spawning/embryo. Includes spawning requirements and requirements of the developing embryo.

2. Fry. Immediately after hatching to size at which they assume adult proportions; i.e., approximately 6.5 cm, according to Franklin and Smith (1960).

3. Juvenile. From 6.5 cm to onset of sexual maturity (beginning of gonadal maturation).

4. Adult. From sexual maturity until death.

Spawning/embryo. Optimal spawning substrate for northern pike is a dense mat of short vegetation (Fabricius and Gustafson 1958) in a shallow, wind-sheltered area. The type of vegetation does not appear to be critical (Fabricius 1950; Forney 1968), although grasses or sedges seem to be preferred (Jarvenpa 1962b; Franklin and Smith 1963; Robertson 1969; June 1971; McCarraher and Thomas 1972). In Nebraska, the greatest densities of eggs were found in flooded prairie grasses at depths of 0.2 to 0.45 m (McCarraher and Thomas 1972). Mowed hay and flooded hay bales were used when flooded natural grasses were not available. Similarly, Forney (1968) found that pike would spawn over prepared plots of winter wheat (approximately 15 cm tall), as well as over natural grasses (Spartina spp.), sedges (Cyperaceae), and water plantain (Alisma sp.). Spikerushes (Eleocharis spp.) and canary grasses (Phalaris spp.) are also commonly used (Franklin and Smith 1963; Forney 1968; Mississippi River Work Unit 1978). Scattered vegetative debris may be used when more preferred substrates are not available (Priegel and Krohn 1975). Crossman (pers. comm.) reported that northern pike in Lake Simcoe (Ontario) often spawn over "finely shredded remains of dead cattails loosely scattered on black muck", and over deciduous leaves from the previous autumn. Most spawning occurs in water shallower than 0.5 m (Williamson 1942; Clark 1950; Fabricius 1950). Northern pike have been observed spawning with their backs out of water (Clark 1950).

The vegetation mat should provide abundant surface area for eggs to adhere to and yet allow the circulation of water. Eggs which fall to the bottom are unlikely to hatch due to anoxic conditions in the organic-rich sediments typical of pike spawning grounds. Northern pike embryos are sensitive to high siltation rates ($\geq$ 1 mm/day), such as occur in waters with extensive wave action and bank slumping (Hassler 1970). The rate of embryo development, the percent normal hatch, and larval vigor are dependent on oxygen availability during incubation (Gulidov 1969; Siefert et al. 1973). A dissolved oxygen concentration of 4.5 mg/l is adequate for embryo development and survival at temperatures up to 19° C (50% saturation) and a low flow rate (30 ml/min); concentrations of 3.2 mg/l (33% saturation) or less appear to be unsuitable for embryos and larvae (Siefert et al. 1973). Gulidov (1969) reported a much higher percent normal hatch for northern pike embryos incubated at dissolved oxygen concentrations greater than 35 to 40% saturation (approximately 4 mg/l at a temperature of 12 to 12.5° C) than for those incubated in lower oxygen tensions.

Hydrogen sulfide may accumulate when the dissolved oxygen concentration is low. Exposure to hydrogen sulfide levels greater than 0.014 to 0.018 ppm for 96 hours decreases the viable hatch of northern pike eggs (Adelman and Smith 1970a).

Incubation time is inversely related to temperature (Swift 1965; Lillelund 1966; Walker 1968). Average length of incubation is approximately 26 days at 6° C, 17 days at 8° C, 12 days at 10° C, 9 days at 12° C, 6 days at 14° C, and 5 days at 16 to 20° C (Swift 1965; Walker 1968).

Temperatures at which development is most rapid are also associated with reduced embryonic and larval survival. Mortality of eggs is high at incubation temperatures greater than 16° C (Swift 1965). Larvae from eggs exposed to temperatures greater than 18° C early in development appear unhealthy (Lillelund 1966). Lillelund (1966) reported maximum hatching success for incubation temperatures between 9 and 15° C and noted that the tolerance of embryos to temperatures outside of this range increases quickly after fertilization. Hokanson et al. (1973) gave an optimal range for incubation of 6.4 to 17.7° C. Most eggs die when temperatures drop to, or remain near, 5° C, but embryos can tolerate diel temperature fluctuations of up to 4° C provided the temperature stays in the suitable range (Hassler 1970).

Fry. The habitat of the embryos becomes the initial habitat of the fry (Franklin and Smith 1963). Dense vegetative cover provides several advantages to larval northern pike (Frost and Kipling 1967). Yolk sac fry have small papillae on the front of their heads with which they can attach to vegetation and remain suspended above the sediments. This keeps the fry removed from dangerously low levels of oxygen, and high levels of H_2S, on the bottom. Hydrogen sulfide concentrations greater than 0.004 to 0.006 ppm (96-hour exposure) decrease growth and survival of sac fry (Adelman and Smith 1970a). Once the yolk sac is absorbed and the fry are ready to feed, approximately 10 days after hatching in Minnesota (Franklin and Smith 1963), the invertebrate fauna associated with the vegetation provides a suitable food base. Thick vegetation also provides refuge from potential predators. Young northern pike are vulnerable to predation from a variety of fishes, including other northern pike (Hunt and Carbine 1951; Alt 1968).

Immediately after hatching, fry are very active (Frost and Kipling 1967; Howard and Thomas 1970). Within the first day, however, most attach to vegetation, where they remain for several days while the yolk sac is being absorbed (Frost and Kipling 1967). In hatchery jars, with no vegetation, fry became quiescent after the initial burst of activity and sank to the bottom (Howard and Thomas 1970).

Fry average 7 to 9 mm in length at hatching (Frost and Kipling 1967; Forney 1968). They begin to emigrate from spawning sloughs when 15 to 20 mm long (Carbine 1942; Franklin and Smith 1963; Forney 1968). The time required to grow to this size is variable. Emigration began 10 to 13 days after hatching in New York (Forney 1968) and 16 to 24 days after hatching in Minnesota (Franklin and Smith 1963).

Emigration may be concentrated or prolonged. Forney (1968) reported that 82, 99, and 37% of the fry left a controlled marsh within 20 days after emigration started, in 3 successive years. Data of Franklin and Smith (1963) indicate similar variability in the length of time for emigration. Most young-of-the-year pike emigrated from a Saskatchewan marsh within a 1-week period, 6 weeks after the completion of spawning (Koshinsky 1979). The reasons for this variability are unclear. Emigration is inhibited by low light intensity; prolonged periods of overcast weather might extend the emigration period (Franklin and Smith 1963; Forney 1968). Other factors, such as water level and food supply, may also determine when the fry depart (Royer 1971).

Growth and survival rates of northern pike fry depend on temperature. Survival is poor at temperatures less than 5.8° C (Lillelund 1966). Growth rate is positively related to temperature for pike fry held at constant temperatures between 7.5° C and 25.6° C, but mortality of 1-day old yolk sac fry increases significantly at temperatures greater than 20.8° C; thus, the rate of net biomass gain is highest at 20.8° C (Hokanson et al. 1973). The rate is high for temperatures from 18.0 to 25.6° C.

Northern pike are spring spawners, and early developmental stages experience a progressively warmer average temperature. Tolerance of high temperatures increases within the embryo and fry stages (Lillelund 1966; Hokanson et al. 1973). The optimal temperature for growth and survival of fry increases from about 21° C shortly after hatching to 26° C after 1 or 2 weeks (Hokanson et al. 1973).

Juvenile. Young of the year and yearling northern pike fed *ad libitum* grew in weight most rapidly at 19° C; maximum growth in length occurred at 21° C (Casselman 1978). Growth rate increased sharply at temperatures greater than 10° C but was positive (about 4% of the maximum) even at 3 to 4° C. No growth occurred above 28° C. The growth rate of yearling northern pike held in small Missouri ponds (average depth = 1.0 m) approached zero during a 3 to 5 week period in midsummer when water temperatures exceeded 27° C (Weithman and Anderson 1977).

Dissolved oxygen concentrations below 7 ppm (77% saturation) resulted in reduced growth rates of juvenile northern pike at a temperature of 18.6° C and a flow rate of 0.24 ml/sec (Adelman and Smith 1970b). The decline in growth rate was gradual down to concentrations of 3 to 4 ppm (33 to 44% saturation) and sharp at levels below 3 ppm.

Young of the year northern pike (12 to 38 g) showed signs of stress when held for 20 to 24 hours at dissolved oxygen concentrations less than 6 ppm (temperature 21 to 22° C) (Petit 1973). Feeding ceased at concentrations of 2 ppm, and none of the test fish survived more than 20 hours at 1 ppm. Test fish held at 1 ppm until they appeared close to death recovered within 24 hours when transferred to water with a dissolved oxygen concentration of 6 ppm.

Adults. Temperature requirements of adult and juvenile northern pike appear to be similar. Maximum growth in length of age 2 and 3 northern pike in an Ontario lake occurred at approximately 20° C; fish of similar age reared in the lab grew best at approximately 21° C (Casselman 1978).

Northern pike in Lake Windermere (England), where water temperatures rarely exceed 21° C (Macan 1970), grew faster in warm than in cold years (Frost and Kipling 1967). Surface water temperature, indexed as the cumulative number of degree-days over 14° C, accounted for 86% of the variation in weight of 4-year old pike, for 16 year-classes. Comparison of scale patterns for northern pike from Waskesiu Lake in northern Saskatchewan with those for pike from several shallow Michigan lakes (Williams 1955) suggests that high summer temperatures may interrupt the growth of northern pike in more southern regions.

Temperatures below 4° C do not appear to be stressful for juvenile or adult northern pike when cooling is gradual (Casselman 1978). In fact, male northern pike in an Alberta lake achieved about 35% of their total annual growth during the winter at temperatures near 1° C (Diana and MacKay 1979). Sudden temperature drops can, however, be lethal. A sizeable northern pike kill occurred when water temperatures in an Alberta lake receiving heated effluent dropped from 21.8° C to 4.9° C within 30 minutes after a power plant shutdown (Ash et al. 1974).

HABITAT SUITABILITY INDEX (HSI) MODELS

Model Description - Lacustrine and Riverine

The Habitat Suitability Index (HSI) models which follow are attempts to condense the preceding observations into a manageable set of habitat evaluation criteria, structured so as to produce an index between 0.0 and 1.0 of overall habitat quality for northern pike. A positive relationship between HSI and carrying capacity of the habitat is assumed (U.S. Fish and Wildlife Service 1981).

Separate HSI models are presented for lacustrine (Fig. 1) and riverine (Fig. 2) habitats, but the two are very similar and are more appropriately described as variations of a single general model. The only differences are that the riverine model contains two additional variables (V_8 and V_9) to account for the availability and accessibility of low velocity habitat, and TDS (V_4) can sometimes be excluded from the riverine model. It is implicit that V_8 and V_9 are not limiting in lentic environments; that is, both would have suitability indices equal to 1.0.

The model includes habitat variables believed to be of general importance in limiting the occurrence of northern pike. The assumed functional relationship between each habitat variable and habitat suitability for northern pike is represented in a suitability index (SI) graph. An SI graph associates SI ratings (on a 0.0 to 1.0 scale) with different levels of an environmental variable. It is assumed that SI ratings for different habitat variables can be compared. Overall habitat suitability is assumed to be determined by the variable with the lowest suitability index; that is:

HSI (lacustrine) = minimum value for suitability indices V_1 to V_7

HSI (riverine) = minimum value for suitability indices V_1 to V_9

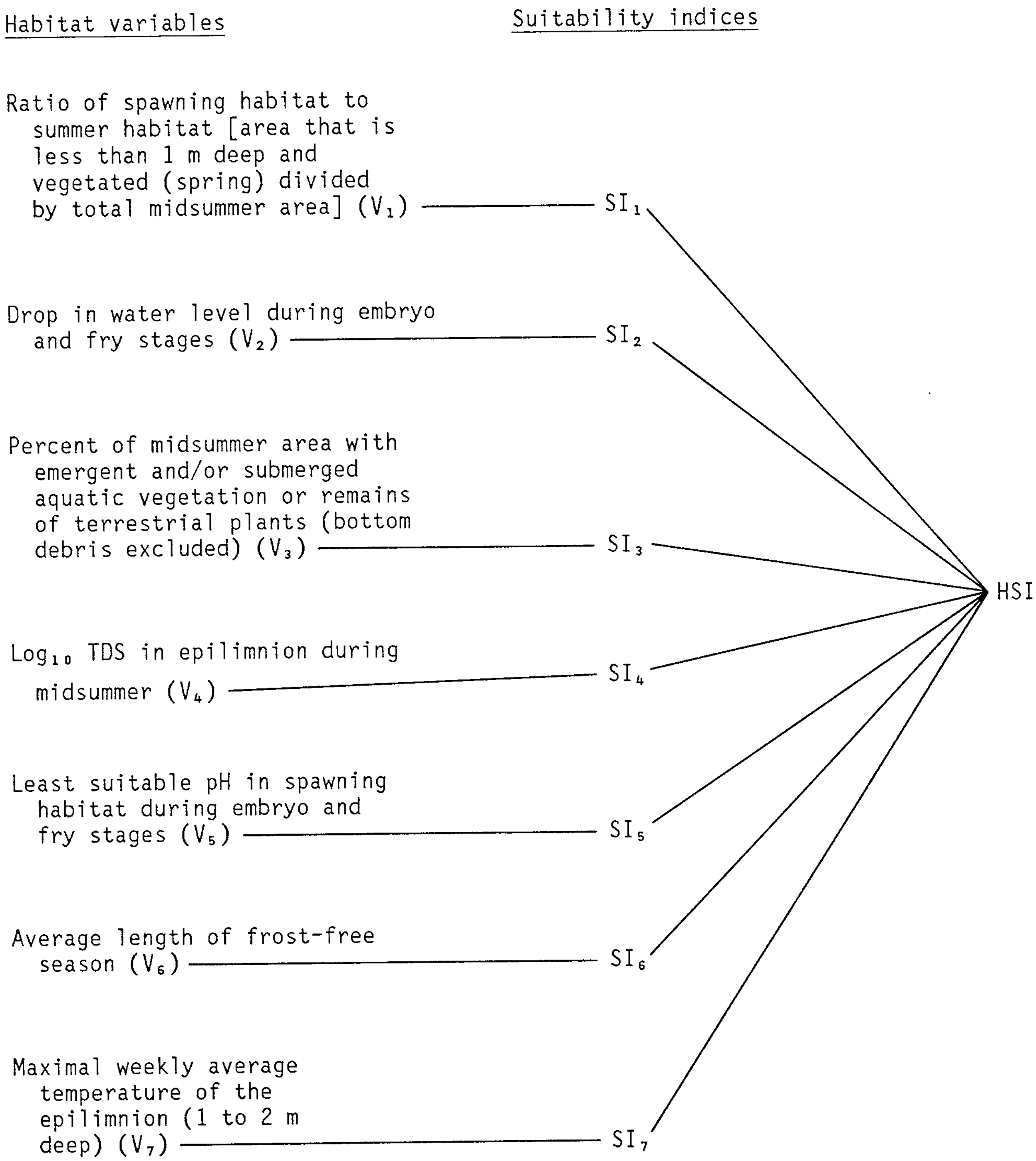


Figure 1. Diagram showing habitat variables included in the lacustrine HSI model for northern pike and the aggregation of the corresponding suitability indices (SI's) into an HSI. HSI = the lowest of the seven suitability index ratings.

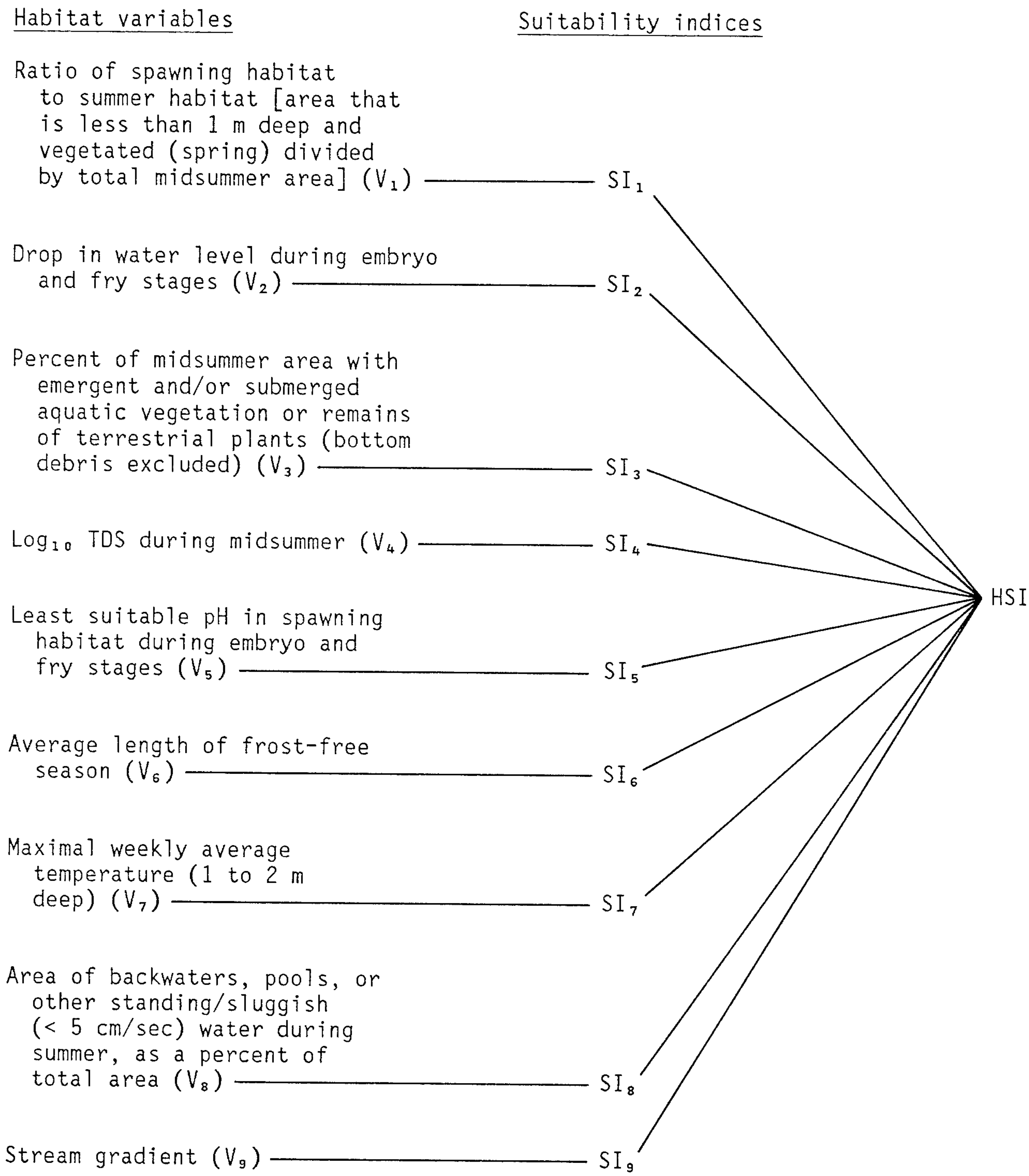


Figure 2. Diagram showing habitat variables included in the riverine model for northern pike and the aggregation of the corresponding suitability indices (SI's) into an HSI. HSI = the lowest of the nine suitability index ratings. V_4 should be eliminated from the model under certain conditions (see p. 24).

The model is designed to assign the highest HSI's to systems capable of producing the most northern pike biomass per unit time on a sustained basis, regardless of how that biomass is apportioned among individual fish. Few long term data are available on production, yield, standing crop, or other measures of population performance for northern pike under different environmental conditions. Therefore, behavioral observations and measures of individual performance, such as growth and survival, were also used to develop suitability index curves for model variables. The rationale and assumptions used to develop the curves are presented in a following section.

Modifications to the model, such as including different or additional variables, may be necessary in some situations. The model is structurally simple, and modifications are easily made.

Model Applicability

Geographic area. The model is applicable to lakes, reservoirs, rivers, and streams throughout North America.

Season. The model is structured to account for seasonal changes in weather and habitat requirements of northern pike and, thus, to indicate the ability of a given habitat to sustain a population on a year-round basis. Overwintering requirements may not be adequately addressed for northern pike in shallow lakes or low discharge rivers that experience extended ice cover (see below).

Cover types. The model is applicable to permanent lakes, ponds, and reservoirs with a mean depth ≥ 1 m during midsummer. It is of doubtful reliability for shallow lakes (even those with mean depths > 1 m) that are covered with ice for long periods. The suitability index graph for V_3 (curve A) is the only part of the model that addresses the possibility of winterkill of northern pike due to low dissolved oxygen concentrations. It is recognized that any single variable is an inadequate indicator of the occurrence and severity of this phenomenon. However, an accurate, general model for predicting winter dissolved oxygen concentrations, based on easily measured or predicted habitat characteristics, does not exist. [The empirical techniques developed by Barica and Mathias (1979) for predicting winterkill in shallow prairie lakes may be useful in some cases.] Because some of the factors that affect the likelihood of winterkill are highly variable from year to year, dissolved oxygen measurements for a single winter do not adequately indicate the likelihood of occurrence of winterkill in a given lake over a series of years. The fact that northern pike can find and use pockets or layers of water with relatively high oxygen concentrations (Magnuson and Karlen 1970; Scidmore 1970) further complicates the modeling problem. Habitats that experience occasional, partial winterkill of northern pike may nonetheless be highly productive of northern pike. Rather than include additional variables with no guarantee of improved model accuracy, it was decided to keep the model simple and emphasize its questionable applicability to potential winterkill lakes. Information presented by Greenbank (1945) and Schneberger (1970)

should help with the identification of such lakes. Material presented in the Habitat Use Information section of this document should allow the construction of a SI graph for winter dissolved oxygen concentration, if such a variable is appropriate for a particular model application.

The model applies to permanent rivers and streams with base flows > 50% of the average annual daily flow and assumes an average depth ≥ 0.5 m in pools and backwaters. Those parts of intermittent tributaries that provide spawning habitat for northern pike residing in a permanent river (or lake) should be included in the determination of V_1, V_2, and V_5.

It is common for northern pike to spend most of the year in a lake or reservoir, but migrate upstream to spawn. In such cases, only the lacustrine model need be applied. The utilization of upstream spawning sites is accounted for in V_1, which includes all accessible potential spawning areas. If, however, both lake and stream habitat are to be evaluated as summer habitat, the riverine model should be used for the stream and the lacustrine model for the lake. The fact that northern pike may utilize spawning grounds at considerable distance from areas inhabited during the rest of the year can make it difficult to establish study area boundaries for rivers, large lakes, or chains of lakes.

Water quality. The model is not applicable to waters overburdened with sewage, those known to contain toxic substances or extreme concentrations of particular solutes, or where heated discharge significantly alters the normal thermal regime.

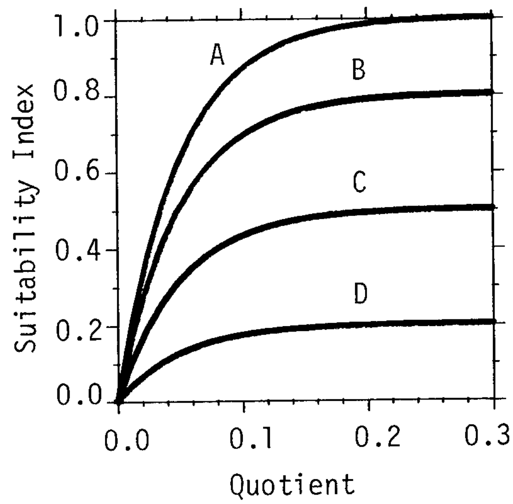
Minimum habitat area. The minimum area required for a self-sustaining population of northern pike is not known. They occur in Ontario lakes as small as 0.4 to 1.4 ha (Johnson et al. 1977).

Other. The model assumes the presence of at least one species of fish that feeds primarily on macrophytes, plankton, macroinvertebrates, and/or detritus. It is not necessary to specify abundance of potential prey species because it is assumed that prey abundance is correlated with general system productivity, as indicated by other model variables.

Verification level. The model represents the author's interpretation of how specific environmental factors combine to determine overall habitat suitability. The model has not been field tested.

Suitability Index (SI) Graphs for Model Variables

Suitability indices for variables in the lacustrine (L) and riverine (R) HSI models should be determined from the following set of curves.

Habitat	Variable		Suitability graph
L,R	V_1	Ratio of spawning habitat to summer habitat [area that is less than 1 m deep and vegetated (spring), divided by total midsummer area].	

Use the appropriate curve, according to the density of vegetation or plant debris within the area included as spawning habitat. Do not include areas covered with filamentous algae, living or dead, as suitable spawning habitat.

A. Vegetation obscures most (> 80%) of the bottom; plant material dense throughout the 15 cm of the water column above the substrate. When submersed, plant material not tightly compacted. Vegetation provides extensive surface area to which eggs may adhere, abundant cover for eggs and fry, and allows for circulation of water around the eggs (e.g., flooded sedge or grass meadow).

B. Plant growth less lush than in A, but covers much of the substrate and occupies much of water column directly above the sediments. More than 60% of the bottom obscured in vertical projection from depth of 15 cm above the bottom. Plant material not compacted when under water.

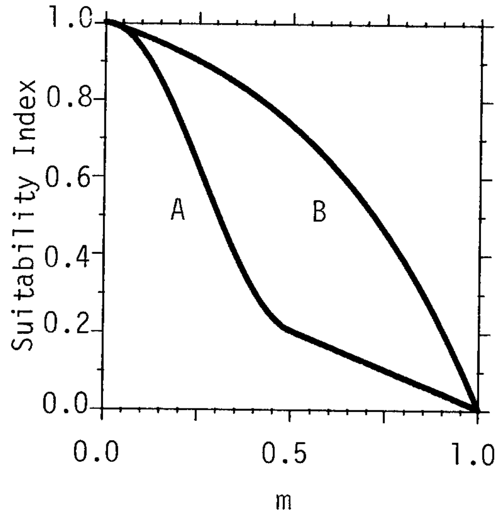
C. Vegetation or debris covers much of the bottom, but plant material does not occupy much of the water column immediately above the substrate. This category may include compacted vegetation, branches of woody plants, and leaves of deciduous trees.

D. Thinly scattered vegetation or debris only. Would provide little, if any, shelter for eggs and fry.

L,R V_2 Drop in water level during embryo and fry stages.

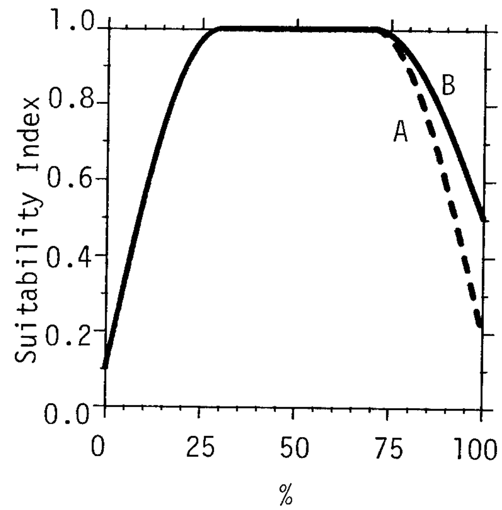
A. Embryo and early fry stages (until yolk sac absorbed).
B. Fry stage, after yolk sac absorbed.

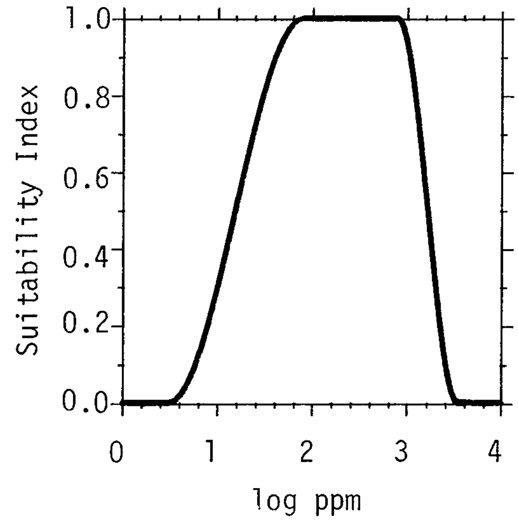
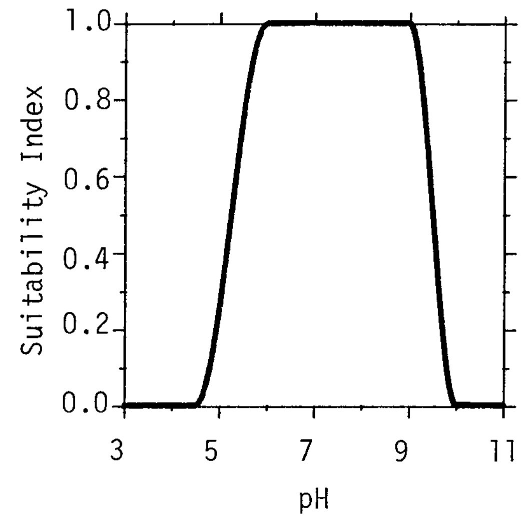
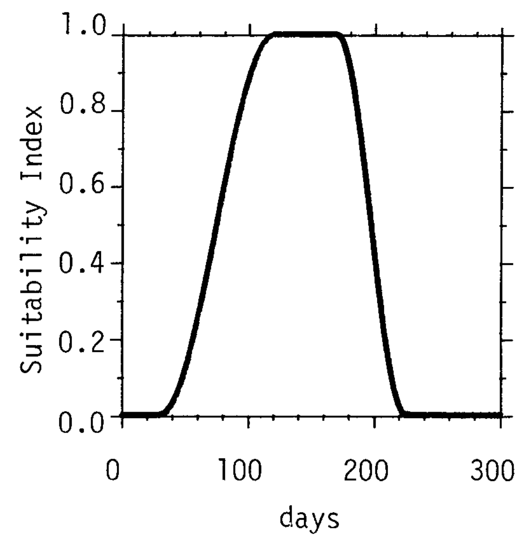
SI for V_2 = A or B, whichever is the lowest.

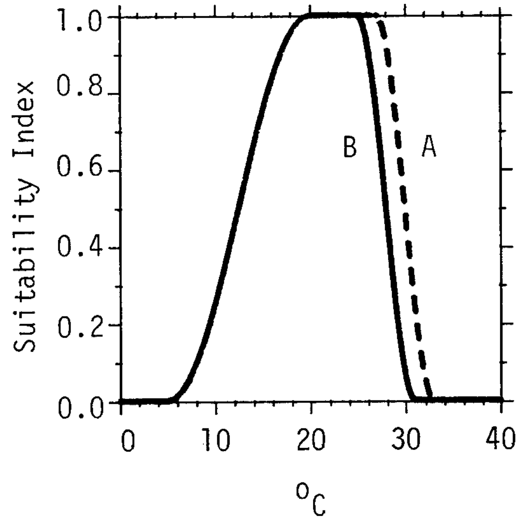
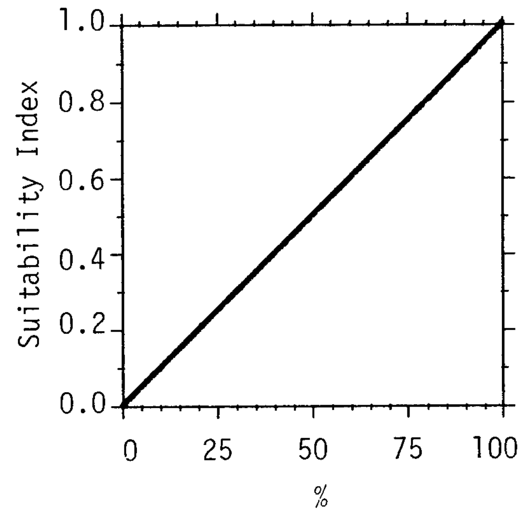
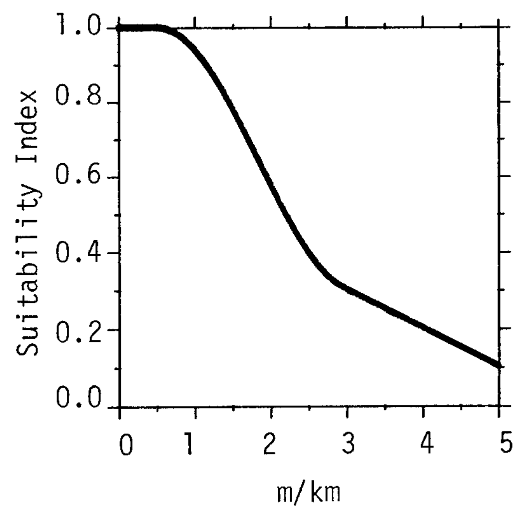


L,R V_3 Percent of midsummer area with emergent or submerged aquatic vegetation or remains of terrestrial plants (bottom debris excluded).

A. Max. depth < 3 m and lake ice-covered > 2 months.
B. Max. depth > 3 m or lake ice-covered ≤ 2 months, or both.



L,R	V_4	Logarithm (base 10) of total dissolved solids concentration of surface waters (1 to 2 m deep) during midsummer.	
L,R	V_5	Least suitable pH in spawning habitat during embryo and fry stages.	
L,R	V_6	Average length of frost-free season (average number of days between last spring occurrence and first fall occurrence of an air temperature of 0° C).	

L,R	V_7	Maximal weekly average temperature of the surface layer (1 to 2 m deep). A. Stratified lake with ≥ 1.5 ppm dissolved oxygen in metalimnion. B. River, stream, unstratified lake, or stratified lake with < 1.5 ppm dissolved oxygen in metalimnion.	
R	V_8	Area of backwaters, pools, or other standing/sluggish (< 5 cm/sec) water during summer, as a percent of total surface area.	
R	V_9	Stream gradient.	

Development of Suitability Index Graphs: Rationale and Assumptions

The preceding suitability index graphs should be regarded as tentative and open to modification. The prospective user should understand that the curves are not the products of extensive laboratory or field investigations. Rather, they reflect the author's subjective integration of the literature, personal experience, and reviewer comments. The following discussion documents some of the thought process that went into constructing the curves. Some curves are better documented than others. In many cases, there is information about preferred and limiting or unsuitable conditions, but little information on which to base ratings of intermediate conditions. No particular significance should be attributed to inflection points unless specifically noted in the text. Straight line segments can be substituted for the sigmoid portions of the curves. The model is offered as a starting point, with the hope that refinements will be made as additional information, including results of testing the model, becomes available.

Ratio of spawning habitat to summer habitat (V_1). Spawning habitat availability is a logical starting point in the development of a habitat suitability index model for northern pike. High spring water levels can create spawning habitat if they flood terrestrial and wetland vegetation. The amount of new spawning habitat that results depends on shoreline topography and the amount of adjacent vegetation. The relative availability of spawning habitat can be estimated by the ratio between the amount of surface area in the spring that is shallower than 1 m and vegetated and the entire surface area of the water body in summer.

The minimum ratio, below which spawning habitat availability limits population size, depends on the carrying capacity, or productivity, of summer habitat. Other model variables account for factors which limit post-fry stages. Therefore, the minimum ratio is estimated for the theoretical maximum density of northern pike. Snow (1978) presented data suggesting a maximum density of 40 pike greater than 35 cm in length per ha (20 kg/ha). Higher densities could not be maintained even though food was plentiful. This maximum density value was used to develop the suitability index curve for spawning habitat availability.

It is assumed that spawning habitat suitability is positively, but asymptotically, related to the area of spawning habitat per spawning female. This means that an increase in the amount of spawning habitat per female is more beneficial when spawning habitat is relatively scarce than when it is plentiful. Limited evidence in support of this assumption is available. Female northern pike have typically been stocked in managed spawning marshes at densities between 5.4 and 23.2/ha (1 fish per 1,847 m^2 and 431 m^2, respectively) (McCarraher 1957; Forney 1968; Royer 1971; Fago 1977). Increasing the density of females from 11.4 to 22.4 fish/ha (5.9 to 17.6 kg/ha) only slightly increased the yield of fingerlings from an experimental marsh in Saskatchewan (Royer 1971). Maximum production from managed spawning marshes in Minnesota was obtained at stocking rates of 11.2 kg of females/ha (Jarvenpa 1962b).

This assumed relationship between suitability and spawning habitat availability must be scaled if it is to be used as the basis for a suitability index curve. Two different scaling procedures were used, one based on spawning behavior and a second based on what appeared to be representative values for fingerling production from managed spawning marshes and subsequent survival through adulthood.

Observations made by Fabricius and Gustafson (1958) under laboratory and natural conditions provide a basis for estimating the area over which eggs of a single "average" female are dispersed. These authors recorded the following observations for pike (< 50 cm) spawning in an aquarium (bottom dimensions: 7.0 m x 0.8 m; depth: 0.4 to 0.5 m) at a temperature of 18° C:

mating frequency, within a series of mating acts: 1.5-2.6 mating acts/min
distance traveled between mating acts: 1 m
average duration of a series of mating acts: 5 min
average interval between successive series: 8 min
(At this time, the pike are at rest.)

Field observations of spawning pike indicated an average mating frequency of 1.7 acts/min, at a temperature of 12° C. This value corresponds to a net rate of movement of 37.5 m/hr. If an average female carries 32,200 mature eggs (Carbine 1944) and sheds an average of 60 eggs/spawning act [the upper limit of the range reported by Svardson (1949)], 537 mating acts would be required before all eggs were deposited. At a rate of 1.7 acts/min, spawning would take at least 5.3 hr and cover a minimum distance of 200 m. If eggs are scattered 0.5 m to either side of the spawning fish, a total area of 200 m^2 (0.02 ha) would be involved. Assuming that spawning groups refrain from spawning where eggs have already been deposited, the minimum ratio of spawning habitat area to summer habitat area can be calculated as follows:

$$\frac{\text{spawning habitat area}}{\text{summer habitat area}} = \text{max. density} \times \%\ \text{females} \times \frac{\text{minimum spawning area}}{\text{female}}$$

$$= \frac{\text{40 pike}}{\text{ha summer habitat}} \times \frac{\text{1 female}}{\text{2 pike}} \times \frac{\text{0.02 ha spawning habitat}}{\text{female}}$$

= 0.40 ha spawning habitat/ha summer habitat, for a population with a balanced sex ratio.

The validity of this approach for estimating spawning habitat requirements depends on the accuracy of several unproven assumptions about northern pike spawning behavior, the density at which crowding occurs on spawning grounds, and the consequences of crowding. An alternative procedure, based on estimates of fingerling production and survival, was tried as a check.

Fingerling production data are available for a large number of managed marshes (Fago 1977). These data show production to be highly variable (7 to

72,000 fingerlings/ha), both among marshes and among years. The median (2,717 fingerlings/ha) was used in the following calculations.

Survival of fingerlings through adulthood is also highly variable. Estimated survival of fingerling northern pike through their first summer was 6%, 22%, and 63% in three successive years (mean = 28%) in a Michigan lake (Beyerle and Williams 1972). Assuming 65% annual mortality thereafter [which seems reasonable for lakes in the conterminous United States, on the basis of data compiled by Carlander (1970)], 9.8% of the fingerlings would survive to age 1+, 3.4% to age 2+, 1.2% to age 3+, and 0.4% to age 4+. Ages 2 through 4 usually account for most of the breeding stock for populations in the conterminous U.S. Assuming a stable age structure and that most mortality occurs between autumn and spring, there would be a total of 0.034 + 0.012 + 0.004 = 0.050 adult fish in the population per fingerling produced in spawning habitat. The minimum ratio of spawning to summer habitat can be calculated in the following way:

$$\frac{\text{spawning habitat area}}{\text{summer habitat area}} = \text{max. density of adults} \times \frac{1}{\text{spawning habitat productivity}}$$

$$\times \text{ fingerlings per adult}$$

$$= 40 \text{ adults/ha summer habitat}$$

$$\times\ 1 \text{ ha spawning habitat/2,717 fingerlings}$$

$$\times\ 1 \text{ fingerling/0.05 adults}$$

$$= 0.29 \text{ ha spawning habitat/ha summer habitat}$$

If it is assumed that most mortality occurs between spring and autumn, then the 1+ fish should be included in the calculation. There would be 0.098 + 0.034 + 0.012 + 0.004 = 0.148 adult fish in the population/fingerling produced, and the minimum ratio of spawning to summer habitat would be 0.10.

Both values are similar to that obtained using the method based on spawning behavior (0.40). An intermediate value, 0.25, is used to develop a suitability index curve. It is assumed that optimal northern pike habitat must have at least 0.25 ha of spawning habitat for each ha of summer habitat. Habitats in which the relative availability of spawning habitat is considerably less than this can still have high suitability index ratings for V_1 because of the asymptotic shape of the suitability index curves.

Type of vegetation in spawning areas is also important. The probability that fertilized eggs will settle on vegetation as they sink depends on vegetation density. Young northern pike also depend on vegetation for protective cover and on the associated invertebrate fauna for food. Lush vegetative cover is ideal; sparse cover is poor. The suitability index for V_1 can be maximal (1.0) only if proper vegetation is present.

Drop in water level during embryo and fry stages (V_2). Northern pike are vulnerable to even slight water level changes during the incubation and nursery periods because they usually spawn in water less than 0.5 m deep and often in water as shallow as 0.1 to 0.2 m. Declining water levels can strand the embryos, fry, and even adults. Embryos are particularly vulnerable because of their immobility. Newly hatched fry become inactive after an initial burst of activity and are, therefore, likely to be stranded by a decline in water level. Once the fry begin to feed, they can probably follow a slowly receding shoreline, provided that the pathway from the spawning area to summer habitat is not blocked. The greater mobility of older fry is the reason for the difference between curves A and B in the suitability index graph. Curve A has a steep slope between 0.1 and 0.5 m because this is the depth range in which most spawning occurs.

Percent of midsummer area with emergent and/or submerged aquatic vegetation or remains of terrestrial plants (bottom debris excluded) (V_3). The extent of vegetative cover is an important component of habitat suitability for northern pike for several reasons. Rooted macrophytes supplement planktonic production and, presumably, increase the food supply for northern pike. Vegetation provides a refuge from predation for young pike and hunting cover for pike of all ages. Complete vegetative cover, however, is probably suboptimal. Northern pike are often associated with the vegetation-open water interface (Reighard 1915). These presumed hunting stations would not be available if the water body were totally covered with vegetation. Furthermore, decomposing vegetation can deplete dissolved oxygen during winter in shallow, ice-covered lakes and rivers with low discharges. It is assumed that optimal habitat would have extensive submerged and/or emergent aquatic vegetation interspersed with open water. At the present time, the model does not contain an interspersion variable.

Logarithm (base 10) of TDS in surface waters during midsummer (V_4). Low levels of TDS usually indicate low fertility, while high concentrations can cause ion regulatory or osmoregulatory stress. A positive relationship between TDS and food supply for northern pike is assumed for TDS values between 0 and 80 ppm. Habitat suitability is assumed to remain constant for TDS levels between 80 and 800 ppm and to decrease at higher levels, with zero suitability for TDS values > 3,500 ppm.

TDS is not a reliable indicator of food supply in most rivers and streams. This variable should be excluded from the riverine model unless TDS is > 800 ppm.

Least suitable pH in spawning habitat during embryo and fry stages (V_5). Northern pike are tolerant of a wide range of pH values but pH can be a locally or regionally important component of habitat suitability. There is no evidence of any adverse effects over the pH range of 6.0 to 9.0. Northern pike reproduction is markedly impaired when pH falls below 5.0. An upper limit is not well defined, but pH levels higher than 9.0 appear to interfere with reproduction. Embryos and fry seem to be more sensitive to pH than do other life history stages.

Average length of the frost-free season (V_6). The length of the frost-free season correlates with the length of the growing season for northern pike; however, if the cold weather season is too short, normal gonadal development may be impaired. The suitability index curve is based on growth data for northern pike, laboratory observations on yellow perch spawning (see text), the relative position of isopleths for length of frost free season (Visher 1954), and the southern limit to the native range of northern pike (Crossman 1978).

Maximal weekly average temperature of surface water (1 to 2 m deep) (V_7). Summer water temperature affects growth and survival of northern pike. The optimal temperature for growth of fingerling and older northern pike is 19 to 20° C (Casselman 1978). Temperatures will be in the optimal range during warming and cooling phases if the maximal summer temperature is slightly higher than the growth optimum. Maximal suitability of V_7 is assumed for peak weekly average temperatures of 20 to 25° C. Laboratory studies show that temperatures over 32° C can kill northern pike within several days (Scott 1964). An oxygenated metalimnion, mouths of tributaries or inlets, or springs may be used when temperatures elsewhere are too high. Their effectiveness as thermal refugia depend on their size and the duration of hot spells.

Percent pools and backwaters during midsummer (V_8) and stream gradient (V_9). Riverine habitat may be suitable to the extent that it resembles a lake environment. Northern pike require standing, or very slowly moving, water. Two variables are included as indicators of the presence of low velocity habitat: percent pools and backwaters during midsummer and stream gradient. A direct, proportional relationship between the availability of standing water habitat (V_8) and habitat suitability is assumed. However, a high gradient stream is likely to be of low suitability even if pools are present, because movement between pools would be restricted. It is assumed that northern pike are less well adapted to high gradient streams than are muskellunge, based on patterns of distribution for the two species (Crossman 1978; Harrison and Hadley 1978). Muskellunge occur in stream reaches with gradients as high as 6.9 m/km (Parsons 1959), but gradients less than 2 m/km seem to be more typical of riverine muskellunge habitat (Brewer 1970; Miles 1978). It is assumed that stream reaches with gradients greater than 5 m/km (0.5%) have little or no habitat value for northern pike.

Field Use of the Model

Year to year variation in weather complicates the application of this habitat model. Such variability is most pronounced for variables related to temperature (V_6 and V_7) and water level (V_1 and V_2). Between-year variation does not pose a problem if the objective of an HSI model application is to obtain an HSI rating for a single year. More often, however, the goal is to obtain an average or representative HSI for a particular body of water that can be compared with HSI's for other bodies of water or for the same body of

water at different times in the future. If it is known that the fluctuation mostly occurs within a range over which the suitability index does not change, then no further consideration of the variability is necessary. Problems arise, however, when stochastic variation in a model variable can result in drastically different HSI's for different years. Ideally, sufficient long term data to estimate probabilities of occurrence of different levels of the habitat variable would be available. The average length of the frost-free season (average number of days between the last spring occurrence and first fall occurrence of an air temperature of 0° C) between 1941 and 1970 is known for many areas in the United States (National Oceanographic and Atmospheric Administration 1978). Average values for selected areas in southern Canada were compiled by Chapman and Brown (1966). Long term water temperature and water level data are also available in some cases. It is recommended that suitability indices used for determination of HSI's be averages of suitability indices corresponding to measured, estimated, or projected conditions over a series of years. Even if long term data are not available, the degree to which water temperature or water level measurements for a single year are "representative" can be evaluated by comparing air temperature, precipitation, and/or stream discharge data for the year in which the measurements were made with corresponding values for preceding years. Climatological summaries and records for U.S. Geological Survey stream gauging stations are possible sources of such information.

Several reviewers had reservations about including V_6 (average length of frost-free season) in the model. The variable is not useful for distinguishing between water bodies that are close to one another and at the same elevation. It is useful when considered over a wider geographic area. If the model is to be applied over a limited area and comparisons of HSI's are to be made only for water bodies within that area, then V_6 can be deleted.

Daily variations in water temperature can be considerable. Daily means, rather than extremes, should be used in this model, because northern pike can tolerate brief exposures to moderately high temperatures. It is recommended that V_7 (maximum weekly average water temperature) be determined by averaging the means of daily minimum and maximum water temperatures for the warmest (water temperature) week of the year. The minimum daily temperature usually occurs sometimes near dawn, and the maximum generally occurs in the early to middle afternoon. Day-to-day monitoring of water temperature is not always possible. Whatever procedure is used to estimate V_7 should account for the daily temperature cycle.

A measurement depth of 1 to 2 m was specified for water temperature (V_7). In cases where curve B is to be used (e.g., unstratified lakes or stratified lakes with < 1.5 ppm dissolved oxygen in the metalimnion), measurements should be made in the littoral zone from 1 m below the surface to the bottom. The most favorable temperature for northern pike, based on the SI curve for V_7, should be used to determine V_7.

Aerial or ground surveys can be used in conjunction with past or projected water level data to estimate spawning habitat availability (V_1) over a series of years. Many plants have luxuriant above-surface growth during summer and early autumn only to die back during late autumn and winter. Spawning habitat quality depends on vegetative cover during spring. Also, if vegetation is examined at a time when it is not under water, its characteristics when submersed should be estimated.

The time and duration of the embryo and fry stages must be determined in order to properly estimate V_2 and V_5. Spawning typically begins when the water temperature reaches 8° C and is usually complete when water temperatures have remained at or above 13° C for several days. Allowing 2 weeks for incubation, 2.5 weeks for fry to grow to the size at which emigration begins, and 3 weeks for most of the fry to depart from the nursery grounds, there appears to be a critical period of 7.5 weeks during which water level drawdowns can affect reproductive success. Absorption of the yolk sac requires about 10 days in Minnesota (Franklin and Smith 1963). The first 3.5 weeks after spawning (incubation and sac-fry stages) would, therefore, seem to be especially critical. These values can serve as general guidelines, but should be revised if there is reason to believe that the critical intervals are different for a particular study site.

The percent of midsummer area covered with vegetation (V_3) and the percent of area as pools, backwaters, or other standing/sluggish water (V_8) can be estimated by following procedures outlined in Terrell et al. (in press).

Several of the variables included in these models do not require field measurements. As noted above, average length of frost free season (V_6) can usually be obtained from a local weather station or from a published climatological summary (National Oceanographic and Atmospheric Administration 1978). If it is necessary to interpolate a value, the relative elevations of the study site and of reference stations should be considered. Stream gradient (V_9) can be calculated from U.S. Geological Survey topographic maps. It is not necessary to measure TDS (V_4) or pH (V_5) if it is known that the measurements would fall within the broad ranges in which suitability indices equal 1.0 or 0.0. Otherwise, the measurement techniques described by Lind (1974) can be used.

Rivers, streams, and surface waters of lakes are usually well-mixed. Horizontal variation in water quality variables, such as temperature, pH, and TDS, are rarely so large as to affect suitability index ratings. Sheltered bays, mouths of tributaries and inlets, and springs are possible exceptions to this generalization. If measurements made at different sites result in different suitability indices, the suitability indices, rather than the raw habitat measurements, should be averaged. Each suitability index should be weighted according to the fraction of the total area over which it is assumed to apply.

The user must decide what part of a body of water is to qualify as "summer habitat". To this point, it has been implied that the entire area would be used. This is not necessarily so. In the case of a large, stratified lake, for example, only that area shallower than the depth of the bottom of the thermocline might be included as as "available habitat". In a river, areas where the velocity exceeds some threshold value might be excluded. If such a preliminary screening step is taken, the decision about limiting the area used as available habitat applies for all model variables. The area included as summer habitat for V_1 should also be used as the total area (that is, the divisor) for V_3 and V_8; the model output (HSI) applies only to this area.

Interpreting Model Outputs

The model described above can generate HSI's to any desired number of decimal places, but it would be misleading to present results to a level of precision greater than ±0.1. The model cannot be expected to discriminate among different habitats with high resolution at this stage of development. It depends on a series of untested assumptions and known oversimplifications. Interactions among model variables and species interactions both play a role in determining habitat quality for northern pike, but these influences are ignored. I recommend interpreting HSI outputs as indicators (or predictors) of excellent (0.8-1.0), good (0.5-0.7), fair (0.2-0.4), or poor (0.0-0.1) habitat.

Habitats with high HSI's would, on average, be expected to have higher standing crops of northern pike than habitats with low HSI's, but a close correlation between population size and HSI is unlikely. Factors not included in this habitat model can also limit northern pike populations.

ADDITIONAL HABITAT MODELS

Aggus and Bivin (in press) used angler harvest as the criterion of habitat suitability and calculated a regression equation relating harvest to reservoir habitat variables for 37 impoundments in the conterminous United States:

$$\text{Log}_{10} \text{ harvest} = 3.7882 - 0.0177 \text{ (growing season)} - 0.8447 \text{ (Log}_{10} \text{ outlet depth)}$$

$$R^2 = 0.67$$

Units are kg/ha (harvest), days (growing season), and feet below a specified elevation (outlet depth). These authors discuss procedures for converting measured or predicted harvest values to HSI's.

Jenkins (1982) calculated the regression equation using mean depth (m), rather than outlet depth:

$$\text{Log}_{10} \text{ harvest} = 3.918 - 0.017 \text{ (growing season)} - 1.425 \text{ (Log}_{10} \text{ mean depth)}$$

$$N = 35$$
$$R^2 = 0.53$$

These regression equations are based on reservoirs with growing seasons ≥ 100 days and outlets between 0.3 m (surface) and 42.7 m deep (Aggus, unpubl. data) and should not be applied to reservoirs that do not met these criteria. It should also be noted that northern pike populations in many of these reservoirs were supported by stocking, so reproductive requirements may not be accounted for in the above equations.

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16. Abstract (Limit: 200 words)

Literature describing the habitat preferences of the northern pike (Esox lucius Linnaeus) is reviewed, and the relationships between habitat variables and life requisites are synthesized into a Habitat Suitability Index (HSI) model. HSI models are designed for use with the Habitat Evaluation Procedures (HEP) in impact assessment and habitat management activities.

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Habit
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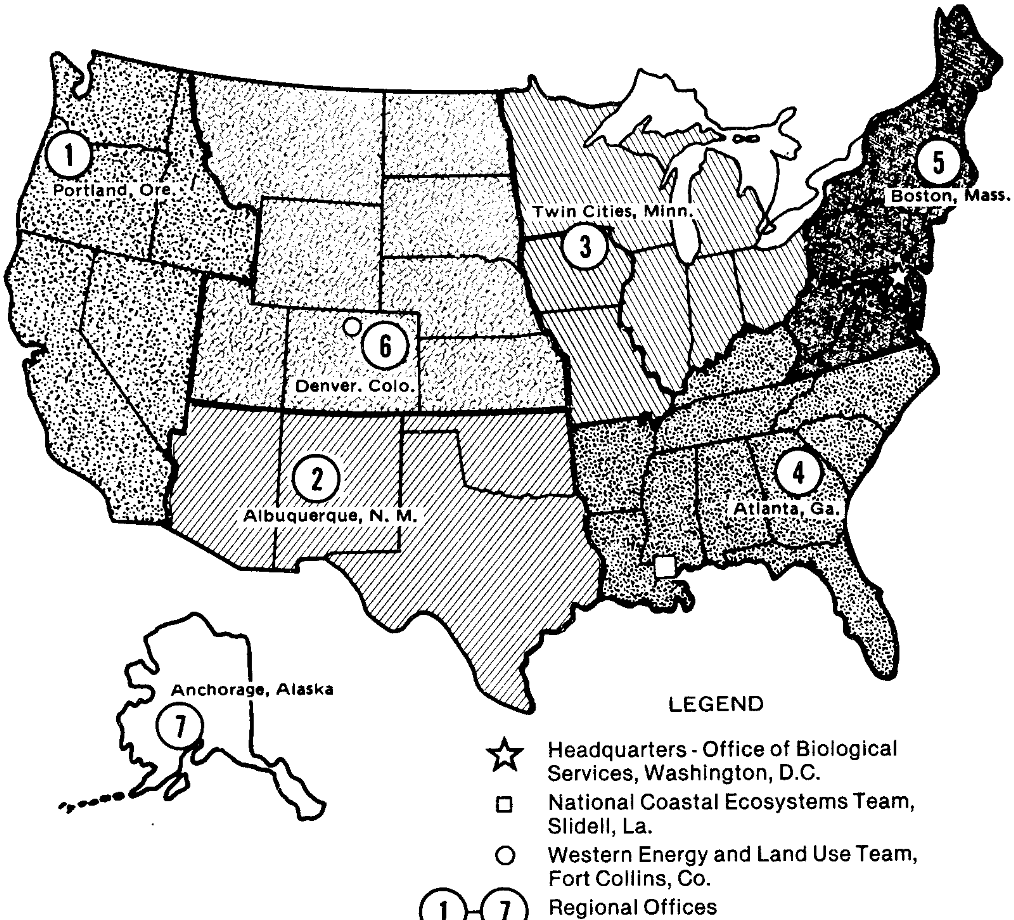

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